Leaf-stem Relationships in the Vascular Plants*

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It is an arresting fact that in the year of our Lord 1942 there is still no general agreement on the organization of the Vascular Plants. Perhaps the nearest one can get to a generalization is the admission that Vascular Plants ordinarily comprise root systems and shoot systems. Studies of the shoot systems indicate the usual presence of stems, leaves and reproductive parts. The interpretation of the relation of leaves to the stem which bears them has been varied. From time to time there have been those who adhered to the phyton hypothesis, a hypothesis that made the leaf the important unit of construction of the shoot system, each leaf consisting of the foliar appendage and its subjacent stem segment or internode. This concept by which the stem becomes a vertical aggregation of leaf bases was probably advocated first by Gaudichaud in 1841, and subsequently by Schultz (1843) and by Delpino (1880, 1883). Little of really scientific contribution could be attributed to these workers. Their fanciful ideas, however, were given an artificial bolstering by Čelakovský (1901) when he brought toegether a group of serious arguments supporting the foliar nature of the stem. However, as Schoute (1931) points out these same facts upon which Čelakovský's arguments were based could equally well be explained otherwise. This early hypothesis did not have a large or literal following. No more did Chauveaud's phyllorhiza hypothesis (1921) a modification of the phyton concept, meet with general acceptance.

Alternative ideas, which held the stem to be an independent organ bearing foliar appendages, have been prominent and generally much more in favor. Our textbooks bear witness to this fact.

With these two concepts of the shoot system in mind, I should like to present the results of certain recent and current developmental studies. Since the work of Buder (1928) and his students (Schmidt, 1924, etc.) on apical meristems there has grown a body of knowledge which challenges the formalized interpretations of developmental patterns in the apices of root and shoot attributed to Hanstein (1868). These studies have been continued especially by the significant works of Schüepp (1926) and Foster (1935, 1936, 1938, 1939a, 1939b, 1940, 1941a, 1941b). The latter investigator has made progress on a comparative study of the diverse types of apical meristems in different plant groups. The already classical works on Helm (1931, 1932) and Louis (.1935) have extended our knowledge of the whole stem tip with its developing leaves. More recently numerous workers have contributed

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to this field,—Priestley (1928, 1929, 1935, 1936) and his associates (Griffiths and Malins, 1930; Majumdar, 1942; Scott and Priestley, 1925), Esau (1938, 1939, 1940, 1942, 1943), Cross (1937, 1939, 1940, 1941, 1942) to name a few. These studies bear directly on any interpretation of the leaf-stem relationship.

Louis reported in detail on the development of the stem apices in nine Angiosperms and one Gymnosperm—*Taxus baccata*. In his study of *Syringa vulgaris*, with opposite leaves, he called attention to the general flat appearance of the apical meristem upon which the paired leaf primordia are elevated (Fig. 1). In their early appearance these peg-like protuberances are composed of cells like those of the meristem itself. At this level a transverse section of the tip indicates an oval or near rectangular shape, with each end of the rectangle called a leaf buttress,—Majumdar's leaf foundation (1942)—on which originates an erect leaf primordium. Such a transverse section Louis (following Schmidt, 1924) considered as made through a *region of maximal area* (Fig. 2). If another transverse section be cut immediately below this pair of leaf primordia, a circular outline is obtained; Louis considers such a circular section as cut through a *region of minimal area* (Fig. 3). A section through the bases of the next lower pair of leaves provides another region of maximal area, with its major axis at right angles to the first. Thus the stem tip is composed of alternating zones of maximal and minimal area, each buttress of the former always bearing a leaf primordium. Obviously then a leaf buttress is topographically a part of the stem with no clear boundary between it and its elevated leaf primordium.

Studies of successive leaves proceeding downward from the apex give one a progressive picture of developmental changes in the leaf. As Louis points out, such studies point to a general increase in vacuolation on the outer or abaxial side of each young primordium and its buttress. Shortly thereafter in each leaf an adaxial area appears as equally vacuolated. Thus in Syringa there is left between the two vacuolated areas, continuous with the apical meristem, a band of tissue as seen in transverse section (Figs. 2, 3, 4).

Careful examination shows this band to be heterogeneous, and comprised of a leaf bundle in procambial stage flanked by residual meristem (Esau, 1943). As one follows the sections downward it is seen that the first two pairs of leaf buttresses completely surround the stem, at which level the four abaxial ground meristems, appearing extensively vacuolated, now envelop the stem as the incipient cortex (Fig. 4). Successive sections also show that each adaxial, highly-vacuolated ground meristem has become continuous with the pith, thereby forming the so-called *leaf gap*.

Thus at a level below the second pair of leaves (Fig. 4) the stem of *Syringa* consists externally of a protoderm surrounding a potential cortex. A pith is clearly evident as an early vacuolated, central ground meristem (Fig. 1, 4).
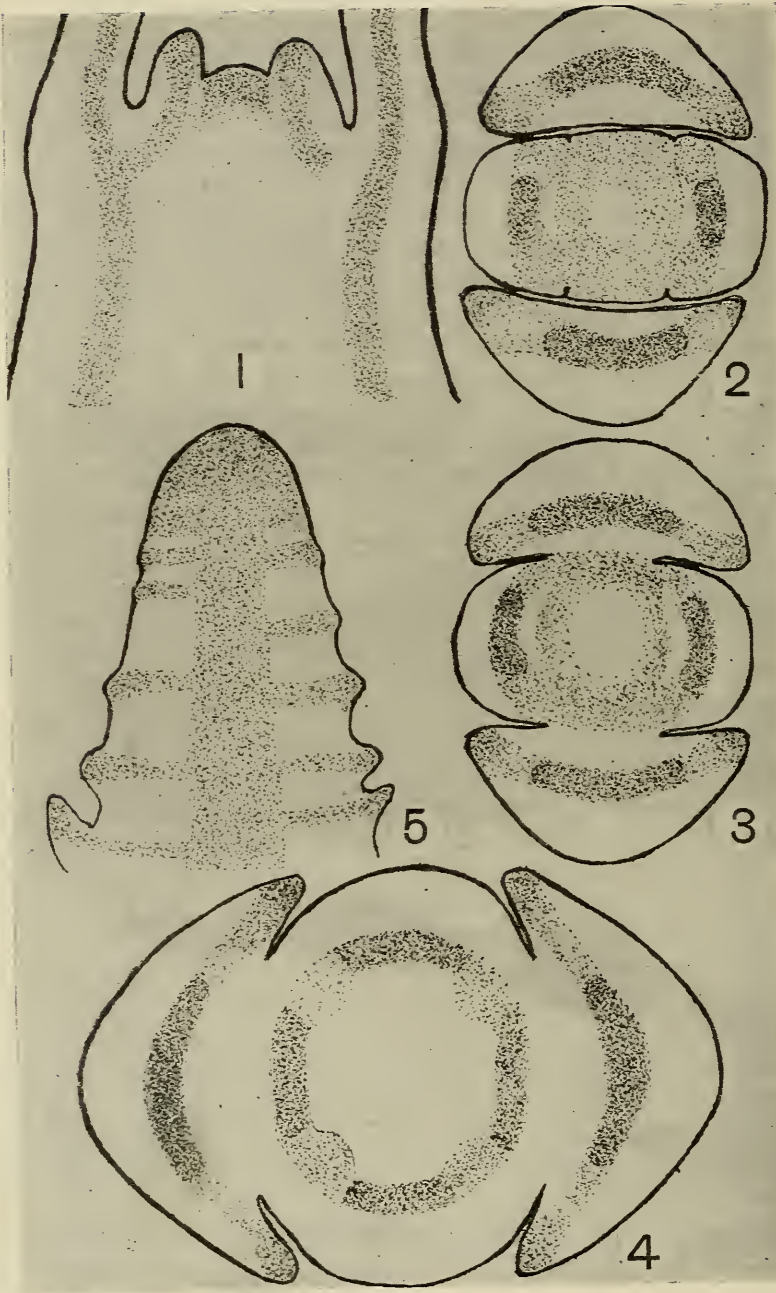
Between these cortical and pith ground meristems exists a ring of small-celled tissue which Louis has designated *prodesmogen*. An examination of this ring, however, shows it to be heterogeneous in nature, not homogeneous as Louis supposed. Confronting each leaf buttress is a small-celled arc of differentially staining tissue—the procambium of the leaf trace—which is continuous with that of the developing leaf. On either side of this leaf trace bundle, in the ring, is a narrow zone of residual meristem,—the *primary ray*. Immediately above each outward-bending leaf trace is the highly vacuolated local break in the ring, referred to above as the *leaf gap* (Fig. 1, right). Louis' investigation of *Syringa* does not include the development of procambium. However subsequent study by the writer indicates the continuity of this procambium with differentiating primary vascular tissue below, its development being continuously acropetal.

Allowing for variations according with the phyllotactic pattern, size of leaf and number of leaf traces per leaf in the large number of Angiosperms now investigated,[*] it would seem fair to state that in this large group of plants vascular and cortical patterns are generally correlated with the formation of leaves at the apex. The pith by contrast seems to belong to the axis. It was on the strength of such studies in his own laboratories that Priestley and his associates propounded the idea of "the unit of shoot growth" for Angiosperms, a modified phyton and a unit closely resembling the "Sprossglieder" of Čelakovský. Each such unit consists of a leaf and a subtending longitudinal sector of the stem—not a whole segment as earlier phytonists had considered it. There are many interesting points in this hypothesis as Priestley has developed it. Time does not permit their consideration. It is true that in the Angiosperms investigated by Priestley the facts could be so interpreted. It is perhaps equally pertinent to question whether the generalization which he makes will hold for all cases in the Angiosperms. In this connection I should like to call your attention to *Hippuris vulgaris,* which Louis has also

[*] Studies by Foster (1938, 1939b, 1940, 1941a, 1941b) and his student Gifford (1943), Crafts (1940), Cross (1939, 1940, 1941), etc., would indicate that this statement is pertinent also for *Ginkgo,* the Cycads, the Conifers and *Ephedra.*

Explanation of figures 1-5

FIGS. 1–4. *Syringa vulgaris.* Fig. 1. Longitudinal section of stem tip (×90). Fig. 2. Transverse section of stem tip showing region of maximal area through buttresses of first pair of leaves (×130). Fig. 3. Transverse section slightly lower through buttresses of first pair of leaves near region of minimal area; leaf gap almost confluent with pith (×130). Fig. 4. Transverse section below attachment of first two pairs of leaves to show the ring composed of procambium and primary rays or interfascicular residual meristem (×130). Fig. 5. Longitudinal section of stem tip of *Hippuris vulgaris* (×130). (Figs. 1-5 after Louis.)
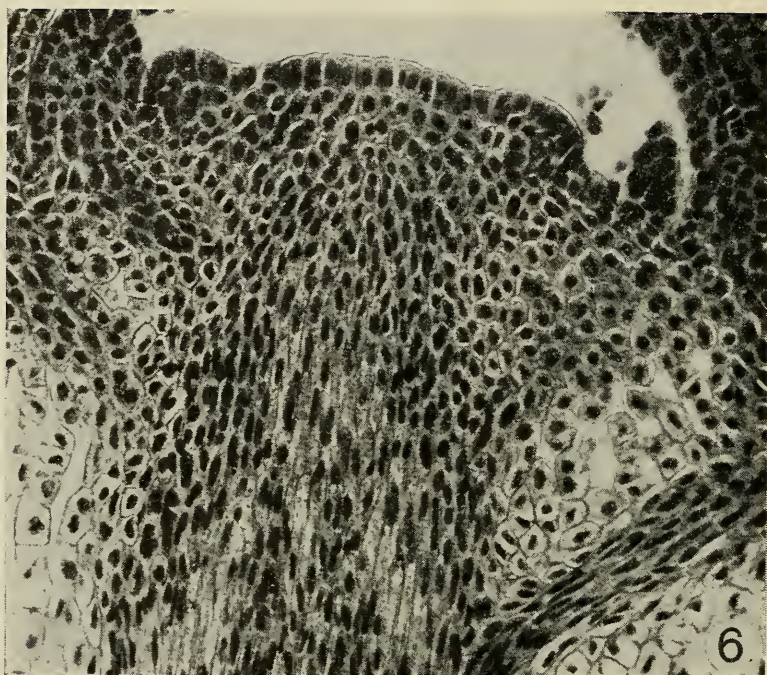
illustrated. As is well known, this plant possesses a protostele in the stem. The apical meristem is not flat as in most Angiosperms; the leaves are borne laterally (Fig. 5). There is a central procambial column—i.e., no pith— which rises above the last leaf primordium. Cortical ground meristem also exists above the highest leaf primordium. In other words, the stem now shows a potential epidermis, a potential cortex, and conducting tissues without the "influence" of leaf primordia.

It may be argued that this aquatic plant is modified in relation to its environment. Possibly so; nevertheless, it seems significant that the plant should be developing at all, if the axis of Angiosperms is a system of phytons or growth units only. On such slight evidence one can do no more than suggest the possibility that Angiosperms have a shoot system, potentially both cauline and foliar, in which ordinarily the leaves possess a dominant and the stems a minor "influence" on development, but in which on occasion the stem may hold the major rôle and the leaves a minor though necessary one. In this connection one might refer to certain seeming cauline bundles—certainly not associated with leaves—which Boke (1941) reports in the cactus *Trichocereus spachianus*.

It is instructive to examine other groups of vascular plants for developmental patterns. Basing one's judgments on the Angiosperms alone may well produce a limited outlook. May I call your attention to the genus *Lycopodium* in which our laboratories have been interested for some time. The conclusions are based on a careful investigation of nine species. Those representatives which we have studied from the Urostachys segregation of *Lycopodium*, *L. lucidulum* Michx. and *L. Selago* L. have a flat-topped apical meristem with erect foliar primordia (Fig. 6). The protostelic vascular cylinder is forecast in a recognizable column of procambial tissue which rises higher toward the apex than the place of origin of the youngest leaf primordium. Young leaf primordia already show procambial strands related to them, never discontinuous with the central column. The cortical ground meristem is belated in appearance. There is never a pith nor is there any adaxial vacuolated ground meristem with its associated leaf gap. By studying successive transverse sections below the apex it is seen that the cauline vascular tissues—the *metaxylem* and *metaphloem*—are outlined or blocked out, within 100μ of the apex in *L. lucidulum*, whereas the first sign of the differentiation of *protoxylem* occurred only about 300μ from the apex. However, though blocked

Explanation of figures 6 and 7

Longitudinal sections of serial stem tips of *Lycopodium* to show proximity of procambial column to the stem apex.   Fig. 6. *L. Selago;* stem apex flat-topped (×260). Fig. 7. *L. sabinaefolium;* stem apex conical (×300).

out, no differentiation of this cauline tissue into metaxylem and metaphloem is seen to occur until after differentiation in the leaf traces themselves has become well established, and then only centripetally from the protoxylem and *protophloem* (Fig. 8). It is interesting to recall that such a blocking out of the metaxylem and metaphloem pattern, before differentiation occurs, is reported commonly in Angiospermous roots. (Esau, 1940; Williams, 1940.)
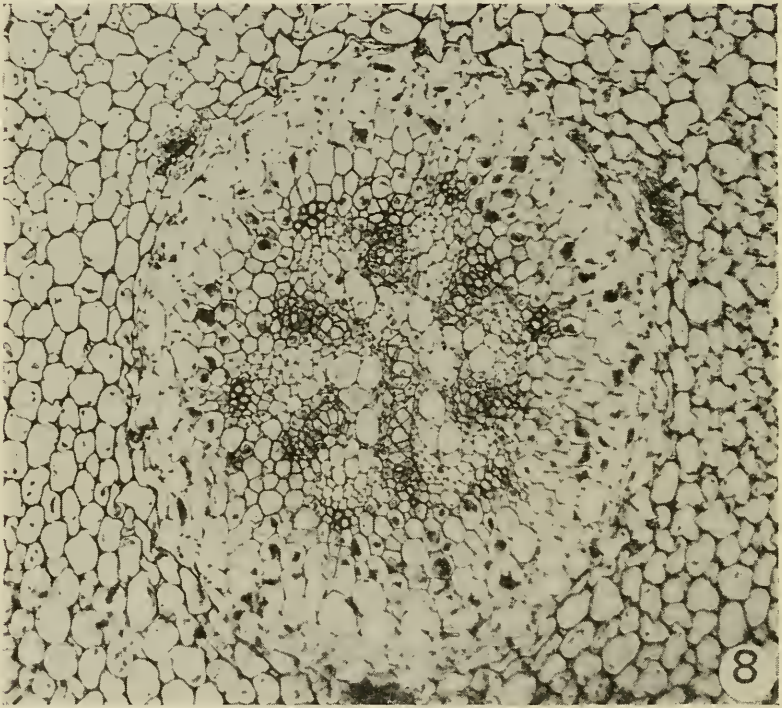

Fig. 8. Tranverse section of aerial stem of *L. sabinaefolium*, 2710μ from apex, showing pattern of the radially organized stele already blocked out, but differentiation only present in the peripheral strands of protoxylem and protophloem (×260).

In the remaining part of the genus *Lycopodium,* as represented by the seven species studied,* the apex is not flat, but conical, with laterally borne leaves (Fig. 7). Here, however, the developmental story is generally the same (Fig. 8). So is it true for the numerous species of *Selaginella* now in process of investigation; the detailed study is not yet complete. Before leaving

* This study includes *Lycopodium inundatum* L., *L. cernum* L., *L. annotinum* L., *L. clavatum* L., *L. obscurum* L., *L. sabinaefolium* Willd., *L. complanatum* L., and its variety *flabelliforme* Fernald.

Lycopodium, I should like to mention that all the underground rhizomes of *L. obscurum* so far examined have only membranous scale-like leaves with no traces. It is significant that this rhizome develops vascular tissues and cortex, however, not dissimilar to those normally present in a leaf-bearing rhizome.

In substance, these living Lycopsida seem to have a shoot system composed of a cauline part with foliar primordia borne initially in either erect or lateral position. Here there seems to be a peripheral set of bundles, which form a primary network and which are connected with the leaves, bundles originating from procambial strands which are truly acropetal and continuous in their origin. In addition, ordinarily differentiating only after leaf connections are established, though blocked out earlier, is the whole central portion of the central cylinder which is cauline in nature and which is never directly connected with the leaves.

What of the Horsetails, Ferns, and Gymnosperms? In *Equisetum,* the story is far from complete. A study of native species of this genus now in progress in our laboratories gives evidence of a continuous acropetally developing procambium to the leaves and branches. It is not yet clear, however, from this work, nor that of Barratt (1920), Queva (1907) or Vidal (1912), just how the nodal ring is developed. Certainly it would be difficult to think of this ring as entirely foliar in nature.

In the Ferns, the study is fragmentary. The work of Gillette (1937) on *Psaronius* and of Schoute (1926) on living Marattiaceae suggest the complicated stele to be of foliar origin. In the three native species of Osmundaceae, as yet unreported studies from our laboratories show no sign of cauline bundles, though Kaplan reports such. In his summary on the Ferns in Verdoorn's MANUAL OF PTERIDOLOGY, Schoute (1938) states (p. 84): "In the Ferns the original Pteridophyte stele with its external sheaths, its phloem and its central solid xylem has been reduced into a mere topographical tissue column, acting as a recipient for leaf-traces, but without any tissue differentiation of its own."

Before leaving the Ferns, I must refer to certain scale-bearing stolons of species of *Nephrolepis,* studied by Lachmann (1885, 1889) and others. Originally described as roots, they proved to be stems with a cortex and a protostelic central cylinder resembling much more that of sporeling Ferns or mature axes of *Gleichnia, Lygodium* or *Hymenophyllum* which remain permanently protostelic.

In the Gymnosperms, the classical account of Koch (1891), followed by those of Barthelmess (1935), Cross (1939, 1940, 1941, 1942), Foster (1938, 1939b, 1940, 1941a, 1941b), Gifford (1943), Korody (1937), and Louis (1935), indicates diverse patterns of apical meristem in the different gymnospermous assemblages. The work is too incomplete to give any summary

statement. Barthelmess (1935), in his study of various Conifers, considers
the primary vascular tissue composed of leaf traces only, variously united
into sympodia. However, his interpretation of procambium developing basi-
petally is not in agreement with Cross' findings (1942) in *Cunninghamia
lanceolata,* Crafts (1940) in *Sequoia,* and our as-yet unpublished findings in
Pinus Strobus and *Ginkgo biloba.* In general, Barthelmess points out the
similarity of the coniferous apical region to that described for the Angio-
sperms by Helm (1931). One observation of Barthelmess' should be referred
to, that of a shoot of *Pseudotsuga* which in the course of its development failed
to produce the normal needle-like leaves and instead gave only membranous,
scale-like structures with no leaf traces. Yet this shoot when examined gives
a normal structural picture for a shoot of *Pseudotsuga* except that the vas-
cular cylinder is unbroken by the usual interfascicular parenchyma or primary
rays.

A summary survey of the literature and current research pertaining to
the organization of primary shoots of diverse groups of the vascular plants
certainly leaves the writer with no final dictum on the nature of the shoot.
There is cumulating evidence, however, that in *Lycopodium* and *Selaginella*
the vascular cylinder is mostly of cauline, to a lesser degree of foliar, origin.
Even here, though blocked out somewhat earlier in development, the differen-
tiation of metaxylem and metaphloem ordinarily does not seem to occur until
the leaf traces are themselves in a process of differentiation.

The evidence for *Equisetum,* Ferns, and Gymnosperms is still too incom-
plete to permit of generalizations. The rhizomes of *Lycopodium obscurum,*
the leafless stolons of *Nephrolepis,* the unusual shoot of *Pseudotsuga,* and
other leafless cauline axes considered by Troll (1937, p. 287–304), give
indication that stems in these groups may develop epidermis, cortex and vas-
cular tissues even though no leaves be present. Certainly the early appearance
of pith in the majority of species of Horsetails, Ferns, and Gymnosperms
would suggest for it a cauline origin, for this pith is often found higher in the
axis than the most apical, foliar, procambial connection. As Schoute (Verdoorn,
1938) points out in his summary for the Ferns, there can be no question as to
the "influence" of megaphyllous leaves on the differentiation of vascular tissues.

In the Angiosperms, developmental studies generally give indication of
the importance of foliar structures on the entire developmental sequence of
events in the axis. There is little evidence to suggest a separate rôle for the
axis in the development of vascular tissues, except possibly in certain aquatics
such as *Hippuris,* possibly in the interesting case of the cactus *Trichocereus,*
and a few other instances. However, the fact that roots develop vascular and
cortical tissues without foliar appendages must not be forgotten.

Is it possible to consider the shoot system as an entity within which a

division of labor has occurred, the leaf being set off physiologically from the axis bearing it even though it originated as a product of the same meristematic activity which adds to the stem tip? There is increasing evidence that in many cases in diverse groups of Vascular Plants each foliar primordium so produced is provided with procambium continuous from below at all times (Esau, 1943; Wetmore and Smith, 1942, etc.). Whatever the later orderly differentiation of primary xylem and primary phloem may be, that continuity seems of significant import. The boundary then between leaf and axis is indefinite with leaf buttresses present as those parts of the axis from which leaf primordia are elevated. It must be pointed out, however, that the "influence" of the leaf is of different degrees in different groups of plants. Certainly in roots, in rhizomes of *Lycopodium obscurum,* in leafless axes of *Nephrolepis,* and in the leafless shoot of *Pseudotsuga,* cortex is produced as well as a vascular cylinder. In the cauline structures, the cortex is ordinarily retarded in its development. In *Lycopodium* and *Selaginella,* microphyllous plants, cortex is ordinarily slow in developing. In the Conifers, one finds needle-like or scale-like small leaves and a slowly developing cortex. In the Angiosperms and Ferns with their characteristic large leaves, cortical and vascular differentiation is early, yet small-leaved types such as *Linum* show the usual delay (Esau, 1942). As Kaplan (1937) has suggested, cortex appears sooner or later but leaves seem to accelerate the process of cortical vacuolation.

If I, this early, should venture to epitomize the leaf-stem situation, it would be something as follows: The early, psilopsid land plants, still leafless, were protostelic. With the advent of leaves, microphyllous or megaphyllous, various changes have occurred in stem organization. Microphyllous plants possess in their primary axes a small amount of "foliar" trace vascular tissue, peripherally connected to the cauline, vascular cylinder. In megaphyllous groups, the foliar vascular system and its stem connections become more significant and the potential cauline portions, failing in varying degrees to differentiate, appear as pith. The shoot system is the sum total of foliar and cauline expression. From the practical point of view, the shoot is still composed of leaves borne on a stem system. From a developmental point of view, where one of necessity is faced with factors underlying development, an understanding of the varied developmental patterns of shoot expression in the vascular plants seems significant. How else can one approach experimentation to determine the underlying physiological and biochemical background than with a knowledge of the structural and developmental variables?

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